TAXONOMIC REVIEW OF THE XANTHISMA SPINULOSUM COMPLEX (ASTERACEAE: ASTEREAE)

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ABSTRACT

A taxonomic review of the Xanthisma spinulosum complex is presented, with county-level (for the U.S.A.) dot maps documenting distribution of the taxa. Xanthisma incisifolium, X. glaberrimum, X. paradoxum (Turner & Hartman) Turner & Nesom, comb. et stat. nov., and X. scabrellum (Greene) Turner & Nesom, comb. nov., do not intergrade with other taxa of the complex and are treated at specific rank. In regions of sympatry, X. spinulosum var. spinulosum, var. gooddingii, var. chihuahuanum, and var. austrotexanum intergrade and are maintained here at varietal rank. Xanthisma spinulosum var. hartmanii Turner & Nesom, var. nov., is described from northern Coahuila, Mexico.

KEY WORDS: Asteraceae, Xanthisma, taxonomy

Xanthisma spinulosum (Pursh) Morgan & Hartman sensu lato is a species complex in the western United States composed of intergrading infraspecific taxa distributed within two subspecies, as treated by Turner and Hartman (1976, as Machaeranthera pinnatifida). Hartman (2006) treated the complex within the genus Xanthisma in his account for the Flora of North America, using recently modified generic circumscriptions as defined by Morgan and Hartman (2003). Nesom reviewed the complex in Mexico (1990) and in panhandle Texas (2003), in each case concluding that one of the taxa was

genetically isolated from the others and justifiably treated at specific rank. Turner (2007) added a taxon at varietal rank from southern Texas, citing collections that appear to represent intergrades with typical *X. spinulosum* in their region of contact. In the present study, we examine geographic distributions in detail and further evaluate biological integrity and taxonomic rank.

Xanthisma glaberrimum at specific rank.

Xanthisma spinulosum var. glaberrimum (Rydb.) Morgan & Hartman was elevated to specific rank as X. glaberrimum (Rydb.) Nesom & O'Kennon (Nesom 2003). Hartman (2006), however, retained the taxon as a variety, noting that "it occurs sympatrically with variety spinulosum in the Texas panhandle, where the two taxa behave like biological species" but that "on the eastern plains of Colorado, however, hybridization and autoploidy have been documented (D.B. Hauber 1986)."

Xanthisma glaberrimum (diploid, 2n = 8) occurs from the southern panhandle region of Texas northwards into southern Manitoba, Canada (Fig. 1). Over most of this region it is confined to mid-grass regions of the central U.S.A. and only rarely comes in contact with populations of typical X. spinulosum (diploid, 2n = 8), which appears to be largely confined to the more western short grass prairies. The two taxa are sympatric in westernmost Nebraska and adjacent Wyoming, southeastern Colorado, and panhandle Texas and adjacent areas of New Mexico and Oklahoma (Figs. 1, 2). Typical X. glaberrimum in southeastern New Mexico mostly grows on gypsum. In DeBaca and Chaves counties, N.M., some plants have a vestiture of barely perceptible tomentum but they contrast sharply in both vestiture and habit with many collections of typical X. spinulosum from the same area.

a. Stems usually unbranched until the upper third, the heads usually distinctly clustered; leaves strictly ascending, narrowly oblong in outline, 1-pinnatifid, midportion 1–2(–2.5) mm wide, lobes oblong-lanceolate to lanceolate or triangular, sometimes shallowly toothed, glabrous or less commonly lightly tomentose, eglandular or less commonly glandular; involucres cupulate..........X. glaberrimum

a. Stems branched from midstem or below to the upper third, the heads diffusely arranged; leaves loosely ascending to spreading, oblong to obovate in outline, especially the basal and lower cauline, 1–2-pinnatifid, midportion 0.5–1.0(–1.5) mm wide, lobes linear to lanceolate, usually shallowly toothed, and glandular to varying degrees, slightly to densely tomentose, rarely without eglandular hairs; involucres shallowly hemispheric......var. spinulosum

Hauber (1986) noted that putatively hybrid tetraploids he investigated in Otero Co., Colo., show intermediacy toward the ascending stems with greatly reduced lateral branching characteristic of X. glaberrimum (vs. the spreading habit with strong lateral branching in var. spinulosum) as well as intermediacy in their degree of light tomentum. Nesom (2003) observed that in panhandle Texas, where X. glaberrimum and X. spinulosum occur as discrete entities in close proximity, the former is typical in morphology but X. spinulosum commonly shows genetic influence of X. glaberrimum. Morphological discontinuity and apparent isolation of the two taxa at local sites were emphasized in the decision to recognize each of the taxa at specific rank. It is plausible that a significant portion of the Texas panhandle populations of X. spinulosum are tetraploid (likely of hybrid origin, as in Hauber's study) and as such, effectively isolated from sympatric, diploid X. glaberrimum. Plants mapped as X. glaberrimum in Colfax Co., N.M. (Averett 345, TEX, Lucas 125, TEX) and in Weld Co., Colo. (Raven & Gregory 19521, TEX) also are intermediate between X. glaberrimum and X. spinulosum, but they probably indicate the close proximity of X. glaberrimum.

Hybridization occurs among well-marked species in many genera (e.g., among *Baptisia* species in Texas, Alston & Turner 1963) and, as in the case here with *Xanthisma*, the occurrence of hybrids does not necessarily make the case for specific negation.

Xanthisma spinulosum var. paradoxum as X. paradoxum.

Xanthisma spinulosum var. paradoxum (Turner & Hartman) Morgan & Hartman is localized in distribution (Fig. 3) and restricted to the Four Corners region, occurring most abundantly in San Juan Co., Utah. It grows on low, rolling, sparsely vegetated hills formed from the Mancos or Fruitland shale formations (Cretaceous), which produce a

substrate of highly alkaline, gypsiferous clay. Common associates include Atriplex corrugata, A. confertifolia, Frankenia jamesii, and Opuntia polyacantha. At least three species are known to be endemic to this area: Sclerocactus mesae-verdae (Boissevain ex Hill & Salisbury) L. Benson, Proatriplex pleiantha (W. Weber) Stutz & Chu, and Abronia bolackii Atwood, Welsh, & Heil (NM Rare Plant Technical Council 1999).

Study of Four Corners Asteraceae by Nesom revealed that morphology of var. *paradoxum* is consistent and discontinuous from that of var. *spinulosum*, even where their distribution slightly overlaps (see couplet immediately below). Many collections of var. *paradoxum* have been made from the vicinity of Hatch Trading Post along Alkali Canyon in San Juan Co., Utah; from that locality, *Porter 1255* (SJNM 4260) is var. *paradoxa*, but *Porter 1255* (SJNM 7252) is var. *spinulosum*. The two Porter plants evidently were collected in close proximity.

Turner and Hartman (1976, p. 314) noted that var. paradoxum "is fairly well-marked and does not seem to intergrade with its more eastern allopatriarch [var. spinulosum], ... it does appear to grade into var. gooddingii to the southwest, although not strikingly so." Var. paradoxum was compared in the original description to var. gooddingii, but as further study has shown, the two taxa are allopatric and do not have the opportunity to hybridize or intergrade. Thus, in parallel with X. glaberrimum, we observe that var. paradoxum is distinct and genetically isolated from X. spinulosum and propose (below) that it be treated at specific rank.

Xanthisma spinulosum var. scabrellum as X. scabrellum.

Turner and Hartman (1976) observed that *Xanthisma* spinulosum var. scabrellum intergrades with *X. arenarium* (Benth.)

Morgan & Hartman to some degree and that *X. arenarium* might with justification also be treated within *X. spinulosum*, although they retained it at specific rank. Both taxa are densely glandular. *Xanthisma arenarium* is restricted to southern Baja California Sur and sympatric there with var. *scabrellum*, which is more widely distributed and extends northward into the adjacent state of Baja California. In southern Baja California var. *scabrellum* apparently is parapatric or slightly sympatric with var. *gooddingii*, which usually is eglandular in the zone of contact with var. *scabrellum*. The two also are conspicuously different in habit. In the current study, we find that neither var. *scabrellum* nor *X. arenarium* intergrades with *X. spinulosum* and, as Shinners did earlier (1950). Consequently, we treat var. *scabrellum* at specific rank.

Xanthisma incisifolium at specific rank.

Plants Xanthisma spinulosum var. incisifolium from a variety of habitats on the islands of San Lorenzo (Baja California) and San Esteban and Tiburón (Sonora) are consistent in morphology and distinct from other X. spinulosum. Xanthisma spinulosum var. gooddingii is the only expression of the species that approaches the geographic range of var. incisifolium and that is sympatric with it (on San Lorenzo and Tiburón). The insular endemic was recognized in a previous study (Nesom 1990) at specific rank as X. incisifolium.

Xanthisma spinulosum sensu stricto and varieties.

We treat *Xanthisma spinulosum* as comprising five varieties. Even with recognition of these geographic variants, *X. spinulosum* var. *spinulosum* is variable, consisting of a panorama of individuals and/or local populations that have received formal taxonomic recognition. Variation within var. *spinulosum* may be complex even within a single county of Texas. For example, at one locality (Taylor Co., 7 mi SW of Merkel), plants of *X. spinulosum* may be found that are completely glabrous with once-pinnatifid leaves (*Henderson 63-787*, TEX), similar to those of *X. glaberrimum*, or that are cottony pubescent with similar leaves (*Henderson 63-785*, TEX). Additionally, plants referable to the "cotula" form (very glandular individuals lacking cottony pubescence) may also occur there, along with various intermediates between the latter and the previously mentioned expressions (LL,TEX). We have recognized all such individuals and/or population segregates in this area

as belonging to var. *spinulosum*. The distribution of densely glandular plants among the collections at LL,TEX is shown in Fig. 4.

Xanthisma spinulosum var. spinulosum intergrades with var. chihuahuanum (Fig. 5) in Mexico, southern Texas, southwestern New Mexico, and southeastern Arizona. In southern Arizona var. spinulosum may intergrade slightly with var. gooddingii (Fig. 7), but this needs detailed investigation. Var. austrotexanum, recently recognized as an endemic of the Rio Grande Valley in southern Texas (Turner 2007), apparently intergrades with var. spinulosum (Fig. 6). Var. hartmanii, first described in the present manuscript, occurs in north-central Coahuila, surrounded on all sides by var. spinulosum (Fig. 5), with which it may intergrade.

Status of subsp. spinulosum and subsp. gooddingii.

Turner and Hartman (1976) treated Xanthisma spinulosum (= Machaeranthera pinnatifida) as having two allopatric subspecies: subsp. gooddingii, a western assemblage including four varieties and a more eastern subsp. spinulosum with three varieties. Morgan and Hartman (2003) informally divided the species into the two subspecies but did not provide a valid combination for subsp. gooddingii in the new generic position. Because we have elevated three of the four original taxa of subsp. gooddingii to specific rank, and because we observe that var. gooddingii (Fig. 7) may intergrade with var. spinulosum and var. chihuahuanum, it no longer seems useful to formally recognize subspecies among the varieties of X. spinulosum treated here.

Key to the taxa of the Xanthisma spinulosum complex.

- 1. Plants eglandular to sparsely or densely glandular, stems usually at least slightly arcuate, with leaves reduced in size near the heads. (3)
- 1. Plants densely stipitate-glandular, stems stiffly erect, branches stiffly spreading-ascending, with leaves even-sized and evenly arranged to immediately below the heads. (2)

- 3. Plants usually glandular to varying degrees, slightly to densely tomentose, rarely without eglandular hairs; stems branched from mid-stem or below to the upper third, the heads more diffusely arranged. (4)
- 4. Involucres mostly 8–15 mm wide (12–22 in var. *gooddingii*); leaves mostly cauline (if basal persistent, then involucres relatively small). (6)
- 4. Involucres 15–25 mm wide; leaves mostly basal or basal and lower cauline. (5)

- 6. Leaves evenly arranged along entire stem, lobes linear, 4–8 mm long, and usually falcate-recurving; heads epedunculate, usually immediately subtended by leaves; stems 30–50 cm high; stems and leaves inconspicuously granular-glandular, without other vestiture.

.....var. hartmanii

6. Leaves usually mostly on proximal 2/3, serrate or with lobes of varying length; heads pedunculate or pedunculate; stems 10–70 cm high; vestiture various. (7)

- 7. Plants evidently coarsely or minutely stipitate-glandular, usually without other pubescence; stems with leaves reduced distally, heads pedunculate; involucres mostly 12–22 mm wide. (9)
- 7. Plants eglandular or very sparsely and inconspicuously glandular, variably villous; stems relatively uniformly leafy up to heads, heads epedunculate; involucres mostly 8–12 mm wide. (8)
- 8. Stems mostly 10–40 cm tall, ascending from the base, intricately branched at midstem; midcauline leaves deeply toothed to divided; persistently thinly floccose tomentose; widespread...var. spinulosum
- 9. Entire plants usually densely and coarsely stipitate-glandular; leaf surfaces dull-textured, lobes and teeth antrorse, not falcate; involucres mostly 12–16 mm wide......var. chihuahuanum
- XANTHISMA GLABERRIMUM (Rydb.) Nesom & O'Kennon, Sida 20:1586. 2003. Sideranthus glaberrimus Rydb. [1900]. Machaeranthera pinnatifida var. glaberrima (Rydb.) Turner & Hartman. Xanthisma spinulosum var. glaberrimum (Rydb.) Morgan & Hartman. Sideranthus laevis Woot. & Standl. [1913]; Haplopappus spinulosus subsp. laevis (Woot. & Standl.) Hall; Machaeranthera laevis (Woot. & Standl.) Shinners.
- 2. Xanthisma incisifolium (I. M. Johnston) Nesom, Sida 20:1585. 2003. *Aplopappus arenarius* var. *incisifolius* I.M. Johnston; *Machaeranthera pinnatifida* var. *incisifolia* (I.M. Johnston) Turner & Hartman; *Machaeranthera incisifolia* (I.M. Johnston) Nesom.
- 3. Xanthisma paradoxum (B. L. Turner & Hartman) Nesom & B. L. Turner, comb. et stat. nov. Based on *Machaeranthera pinnatifida* var. *paradoxa* B. L. Turner & Hartman, Wrightia 5:314. 1976.

Type: USA. Colorado. Montrose Co.: Paradox, 21 Jun 1912, *E.P. Walker 147* (holotype: NY!, internet image!; isotypes: DS!, GH!, US! internet image!). *Xanthisma spinulosum* var. *paradoxum* (B. L. Turner & Hartman) Morgan & Hartman.

Stems numerous from base, ascending, 6–15 cm high, stems and leaves thinly tomentose-puberulent, eglandular. Leaves: basal persistent and dense, cauline mostly on proximal half of stems, basal and cauline deeply dissected, lobes linear, spreading-ascending. Heads on naked or bracteate peduncles 15–40 mm long; involucres cupulate, mostly 15–25 mm wide; phyllaries linear-lanceolate, minutely puberulent and finely granular-glandular.

Washes, clay hills, sandstone, disturbed sites, desert scrub, pinyon-juniper. Arizona, Colorado, Utah; 1400–1800 m; (Mar–)Apr–Oct; Arizona, Colorado, Utah.

4. XANTHISMA SCABRELLUM (Greene) Nesom & B. L. Turner, comb. nov. Based on *Eriocarpum scabrellum* Greene, Erythea 2:108. 1894. Type: Mexico. Baja California: Los Angeles Bay, 1887, E. Palmer 539 (holotype: ND-G?; isotypes: US-2 sheets! internet images!). Machaeranthera scabrella (Greene) Shinners; Xanthisma spinulosum var. scabrellum (Greene) Morgan & Hartman; Machaeranthera pinnatifida var. scabrella (Greene) B. L. Turner & Hartman.

Plants with a woody caudex; stems, leaves, and phyllaries densely stipitate-glandular. Stems usually spreading from the base, (6-) 15-35(-45) cm tall. Leaves oblong oblanceolate, 5-25 mm long, 1-3 mm wide, relatively even-sized along the stems (smaller immediately beneath heads), shallowly but coarsely toothed. Heads on peduncles 0-5(-10) mm long; phyllaries usually spreading to recurving at apex. 2n=8, 16.

Sandy roadsides, rocky slopes, shrublands, thorn-forests, short-tree woodlands, 10–400 m; most commonly Jan–Apr but sporadically all seasons; Baja California Sur, Baja California.

- 5. Xanthisma spinulosum (Pursh) Morgan & Hartman, Sida 20:1406. 2003. *Amellus spinulosus* Pursh (not *Machaeranthera spinulosa* Greene).
- 5a. Var. AUSTROTEXANUM B. L. Turner, Phytologia 89:350. 2007 [nom. nov.]. Based on *Haplopappus texensis* R.C. Jackson; *Machaeranthera texensis* (R.C. Jackson) Shinners.
- 5b. Var. CHIHUAHUANUM (B. L. Turner & Hartman) Morgan & Hartman, Sida 20:1408. 2003. *Machaeranthera pinnatifida* var. *chihuahuana* Turner & Hartman 2n = 8, 16.
- 5c. Var. HARTMANII B. L. Turner & Nesom, var. nov. TYPE: Mexico. Coahuila. 85 mi from San Miguel on Muzquiz road, common along road beneath *Acacia* with *Hymenoxys*, *Sorghum*, *Verbena*, *Lantana*, *Aristida*, 24 May 1972, *R.L. Hartman 3333*[c] (holotype: TEX!; isotypes: TEX, RM).

A *Xanthismo spinuloso* var. *spinuloso* distinctus foliis profunde dissectis lobis linearibus falcato-recurvatis.

Stems and leaves inconspicuously granular-glandular, otherwise glabrous. Leaves relatively even-sized and similar in morphology from base of stem to heads, 2(-3)-pinnately parted with linear and usually falcate-recurving lobes. Heads usually immediately subtended by leaves.

Additional collections examined. Mexico. Coahuila. 1 mi W of La Rosita on road to Muzquiz, common in stream bed, 24 May 1972, *Hartman 3334* (LL, RM). 3 mi W of Rancho La Rosita, 43 mi NW of Muzquiz, E of Sierra de la Encantada, 22 May 1968, *Powell, Patterson & Ittner 1577* (TEX - 2 sheets).

These plants have been collected from only a single small area in north-central Coahuila -- they are highly distinct in a morphology not seen anywhere else in the range of the species. Three separate collections indicate the morphology is consistent. Collections of *Xanthisma spinulosum* from around the city of Muzquiz (*Marsh 196*-

TEX, Marsh 1196-TEX), about 55 kilometers southeast of typical var. hartmanii, have leaves more deeply dissected than normal and it is possible that these plants show genetic influence of var. hartmanii. On the other hand, their leaves are smaller and less dissected than in var. hartmanii and their vestiture is densely tomentose. Otherwise, plants surrounding var. hartmanii in all directions in Coahuila are var. spinulosum. It is plausible that further field study may show that var. hartmanii would be appropriately treated at specific rank.

5d. Var. GOODDINGII (A. Nels.) Morgan & Hartman, Sida 20:1408. 2003. Sideranthus gooddingii A. Nels.; Machaeranthera pinnatifida var. gooddingii (A. Nels.) B. L. Turner & Hartman

Baja California plants are slightly tomentose but completely eglandular or nearly so, while those of Sonora northward into the U.S.A. are minutely stipitate- to granular-glandular and have consistently narrower leaves. The tall and erect stems, large heads, linear leaves with long, sharp teeth, and distinctive vestiture of var. gooddingii are distinctive. It is maintained here within Xanthisma spinulosum because of putative intergrades with var. spinulosum, but these two taxa may prove to be isolated. 2n = 8.

5e. Var. SPINULOSUM

Diplopappus pinnatifidus Hook.; Machaeranthera pinnatifida (Hook.) Shinners.

 ${\it Sider anthus\ cotula\ Small;\ Haplopappus\ spinulosus\ subsp.} \ cotula\ (Small)\ H.M.\ Hall$

2n = 8, 16.

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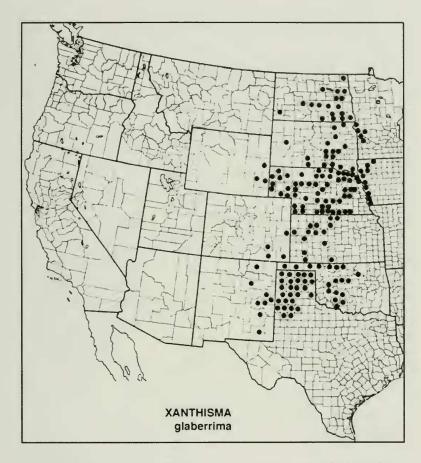


Fig. 1. Distribution of Xanthisma glaberrimum by county in the U.S.A.

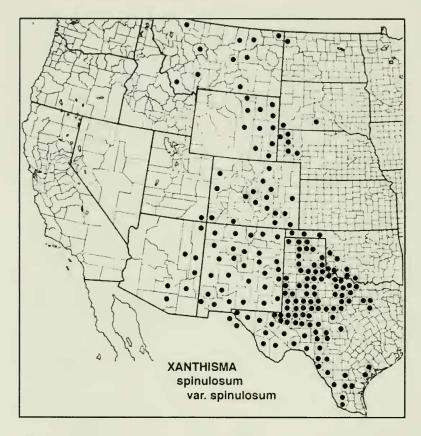


Fig.2. Distribution of *Xanthisma spinulosum* var. *spinulosum* by county in the U.S.A.

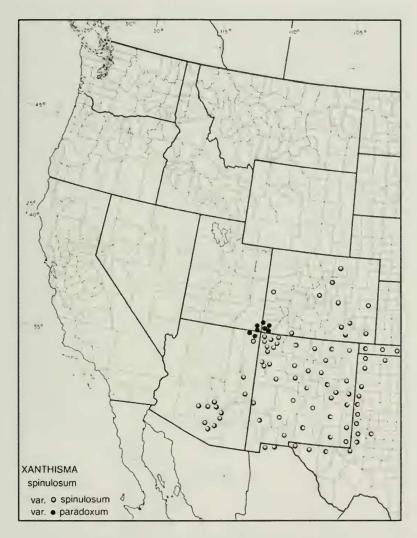


Fig.3. Distribution of *Xanthisma spinulosum* (open circles) and *X. paradoxum* (closed circles) in the Four-Corners region of the southwestern U.S.A.

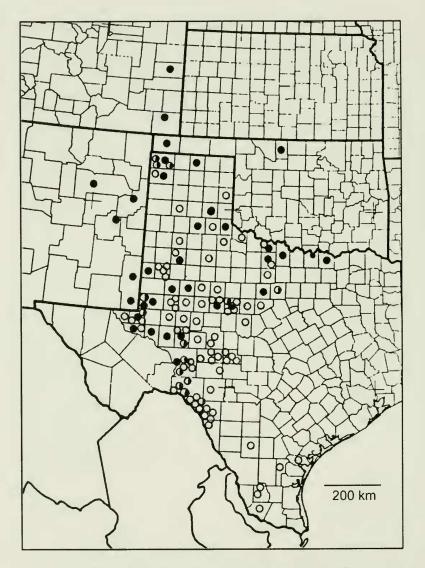


Fig.4. Distribution of plant and/or population forms of *Xanthisma* spinulosum in the southcentral U.S.A.: var. spinulosum (open circles); "cotula" form (closed circles); intermediates (half circles).

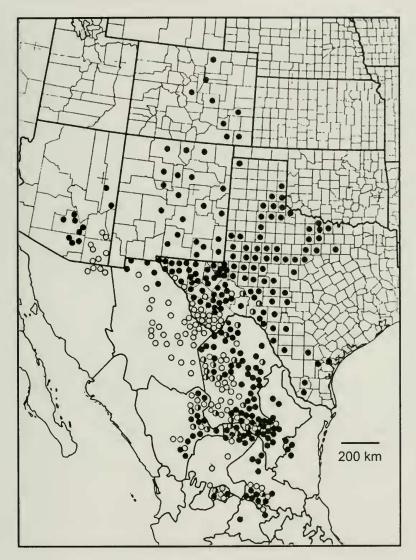


Fig.5. Distribution of *Xanthisma spinulosum* in the southwestern U.S.A. and closely adjacent Mexico: var. *chihuahuanum* (open circles); var. *spinulosum* (dotted circles). Var. *hartmanii* is not mapped.

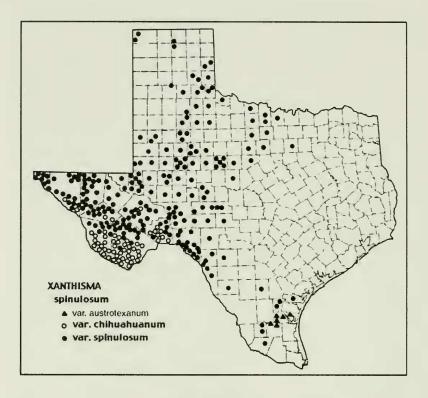


Fig.6. Distribution of *Xanthisma spinulosum* in Texas: var. austrotexanum (triangles); var. chihuahuanum (open circles); var. spinulosum (closed circles).

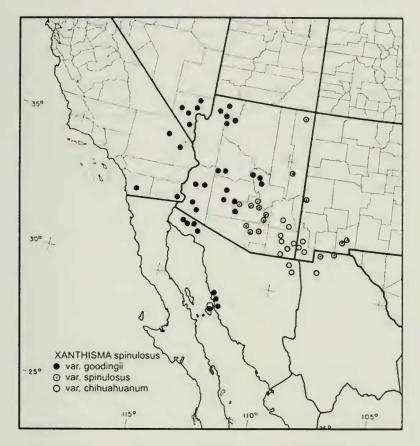


Fig. 7. Distribution of *Xanthisma spinulosum* var. *gooddingii* (closed circles).